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PB-259 689-T

Some Regularities in Absorption of Sulfur Dioxide by Woody Plants

Environmental Protection Agency, Research Triangle Park, N C

1971

BIBLIOGRAPHIC DATA SHEET	1. Report No. EPA TR75-19	2.	3. Recipient's Accession No.
4. Title and Subtitle: Some regularities in absorption of sulfur dioxide by woody plants.			5. Report Date: 1971
			6.
7. Author(s): V.S. Nikolayevskiy			8. Performing Organization Rept. No.
9. Performing Organization Name and Address: TRANSLATED FROM RUSSIAN BY EPA			10. Project/Task/Work Unit No.
			11. Contract/Grant No.
12. Sponsoring Organization Name and Address: Translation Service, Office of Administration - Library, Research Triangle Park, NC 27711			13. Type of Report & Period Covered
			14.

15. Supplementary Notes: Proceedings: Perm Order of the Red Banner of Labor A.M. Gor'kiy State University, 227(5) 1971, pp.29-35.

16. Abstracts

17. Key Words and Document Analysis. 17a. Descriptors

EPAISD

17b. Identifiers/Open-Ended Terms

AIR POLLUTION - EFFECTS ON PLANTS AND ANIMALS

17c. COSATI Field/Group 06F 57H

18. Availability Statement: THIS TRANSLATION WAS MADE FROM A NON-COPYRIGHTED TEXT.	19. Security Class (This Report): UNCLASSIFIED	21. No. of Pages: 14
	20. Security Class (This Page): UNCLASSIFIED	22. Price: $3.50

321026

PB 259 689-T

EPA - TR 19-75

SOME REGULARITIES IN ABSORPTION OF SULFUR DIOXIDE BY WOODY PLANTS

[Nekotoryye zakonomernosti poglosheniya sernistogo gaza drevesnym rasteniyami]

by

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Published in Uchenyye zapiski Permskogo ordena trydovogo krasnogo znamenii gosudarstvennogo universiteta im. A. M. Gor'kogo [Proceedings, Perm Order of the Red Banner of Labor A. M. Gor'kiy State University, 277(5) 1971, pp. 29-35]

The thought of the dependence of gas resistance on rate of absorption of toxic gases is becoming stronger and stronger among investigators (Krasinskiy, 1950; Nikolayevskiy, 1963, 1969; Greshta, 1970). Our studies, using labeled sulfur dioxide (Nikolayevskiy, et al., 1971) established that the susceptibility to injury of leaves by sulfur dioxide, in trees, flowers, lawn grasses and weeds, is directly proportional to the rate of absorption of the gas and formation of a lethal dose. The rate of absorption of sulfur dioxide in nonresistant species is 2-5 times and more than that of resistant ones. On the other hand, a statistically significant

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Translated for NERC Library, EPA, by LEO KANNER ASSOCIATES, P. O. Box 5187, Redwood City, California 94063, (415) 365-3046, November 1974.

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inverse correlative connection has been established in woody plants, between the number of stoma per mm^2 and susceptibility to injury by sulfur dioxide (Nikolayevskiy, 1966, 1967). By means of the infiltration method, we determined the daily dynamics of movement of stoma in 5 species of woody plants (Nikolayevskiy, 1963, 1964). It was determined that, not only are the stoma smaller in resistant species, but they are open a shorter time in the course of a day. A considerable portion of the day, they are either half-closed (xylene passes through) or almost covered (benzene passes through the intercellular space). The hypothesis was expressed that the number and sizes of stoma in resistant species and the nature of their movement in the course of a day allows them to regulate the rate of absorption of sulfur dioxide, which was confirmed in tests of accumulation of labeled gas by the leaves. Moderately resistant and nonresistant species were incapable of regulating the rate of gas exchange and SO_2 absorption during a day to the same extent as resistant ones, because of the significant opening of the stoma. Moreover, there is a considerably greater volume of intercellular space in the spongy parenchyme and, consequently, a larger absorption surface in the nonresistant species. As a consequence of the rapid absorption of the gas by nonresistant species, a higher SO_2 concentration gradient is formed (in the mesophyll and on the outside of the leaves), which leads to an increase in diffusion of the gas. The SO_2 concentration gradient is higher in nonresistant species and lower in resistant ones, which correlates directly with susceptibility to damage of the leaves.

Thus, experimental data obtained, by means of modern isotope methods using $C^{14}O_2$ and $S^{35}O_2$ have demonstrated the presence of the direct, almost

functional dependence of susceptibility to damage of plants by sulfur dioxide on the rate of absorption of the gas and formation of a lethal dose.

At the same time, some contradictions are being found between the number and sizes of stoma in plants and the rate of diffusion of gas through them. According to contemporary conceptions (Maximov, 1958), the rate of diffusion of a gas depends, not only the area of the stoma, but on their diameter or perimeter. Thus, in accordance with these considerations and, taking the number and sizes of the stoma into consideration, there should be a higher gas diffusion rate in the resistant species. As has already been stated above, isotope methods and susceptibility to damage of plants by gases do not confirm this. In our opinion, this contradiction can be explained, if it is taken into consideration that the diffusion patterns were determined by Stefan (cited by Maximov, 1958), not on living plants, but on nonliving model systems. It is evident that the gas diffusion rate in plants will be determined, not only by the number and size of the stoma, but by a whole series of additional factors: the presence of intercellular spaces in the spongy parenchyme of the leaf, the area of the absorbing surface of the mesophyll cells, the gas concentration gradient and the temperatures outside and inside the leaf, the presence of a counter-current transpiration flow through the stoma, etc. The contradiction between the number of stoma and the gas exchange rate can be explained, if the rule of Stefan (Maximov, 1958) for stoma and new events contained in the work of V. A. Gorbavtsov (1970) are taken into consideration. In accordance with the rule of Stefan, the rate of flow of the gas through the stoma does not depend on the number of stoma and the diameters of the stomatal slits, but, with constriction of the stomatal slits by a half or

more, a certain proportional relation of diffusion on degree of constriction is observed subsequently. If it is considered that the dimensions of the stoma and stomatal slits of resistant plants are almost half the size and less and are opened for a shorter time during the course of a day, the difference between species is indisputably significant and can affect the rate of gas diffusion. New conclusions, which are of interest for understanding the mechanism of gas absorption by plants, not only as a process of diffusion through the openings in the stoma, but by means of transport in the pellicular layer of moisture, are contained in the article of V. A. Gorbavtsov (1970). He considers that gas exchange of a leaf depends, not only on the geometric parameter, but on the physical-chemical properties of the cell membrane surfaces and the physiological processes in the plants. We have attempted to determine the dependence of susceptibility to damage of plants on the daily dynamics of movement of the stoma, illumination and reaction of the stomatal apparatus to the effect of sublethal concentrations of SO_2.

Experimental Procedure

The degree of opening of the stoma was determined by the infiltration method, three times a day (at 8:00 a.m., 1:00 p.m. and 6:00 p.m.), of 42 species of woody plants. Penetration of alcohol into the intercellular space (arbitrary 3 points) means that the stoma are open; penetration of benzene (2 points), half-open, and of xylene (1 point), almost closed. Branches in flasks containing water were placed in a 125 l polyethylene chamber for 1 hour, into which 100 ml of 100% SO_2 was introduced by a syringe. Susceptibility to damage was determined after 4-5 hours according to N. P. Krasinskiy (1950). The effect of SO_2 on the stomatal apparatus

was determined by the infiltration method, after gasing, in the morning test.

Experimental Results

On the day of the test, 22 June 1970, and on the preceding days, the weather was hot and sunny, which is important for revealing differences in movement of the stoma and susceptibility to damage, since increased solar radiation increases plant damage. The daily average indices of susceptibility to damage of species were arbitrarily divided into three groups, according to N. P. Krasinskiy (resistant, moderately resistant and nonresistant), and the indices of the degree of opening of the stoma are presented in Table 1, for species and resistance groups. Some differences in the location of species by resistance group, compared with preceding studies (Nikolayevskiy, et al., 1969), are connected with some special weather conditions in the summer of 1970.

It is clear from Table 1 that, in the morning hours, woody plants are damaged 2-22 times less than in the daytime and evening. In the middle of the day, susceptibility to damage of the plants, at identical initial concentrations, increases and it decreases in the evening. The latter may be connected with the effect of light, as a source of energy for photodynamic oxidation processes in the cells under the influence of SO_2, since the extent of opening of the stoma is negligible during the day. In the majority of cases, the location of species by susceptibility to damage was similar in both the morning and the daytime and evening hours.

Box elder, Tartar honeysuckle, balsam poplar and white willow are exceptions.

TABLE 1

SUSCEPTIBILITY TO DAMAGE OF LEAVES OF WOODY PLANTS VS. DEGREE OF OPENING OF STOMA*

a Виды и группы растений	b Повреждаемость в % листовой поверхности				c Степень открытия устьиц в баллах				
	d в 8 час.	e в 13 час.	f в 18 час.	g Средняя за день	d 8 час.	e 13 час.	f 18 час.	g Средняя за день	h После действия SO_2 в 8 час.
i **Устойчивые виды**									
j Вяз обыкновенный	0	0	0	0	0	0	1	0,3	0,0
k Жимолость татарская	0	56,5	0	18,7	2	1	2	1,6	0,0
l Бересклет европейский	0	—	5,5	2,7	3	2	3	3,0	2,0
m Клен ясенелистный	0	38,5	22,0	20,2	1	3	1	1,3	0,0
n Черемуха обыкновенная	0	35,0	5,0	13,0	2	0	1	1,0	1,0
o Сирень обыкновенная	0	2,0	37,0	13,0	3	2	2	2,3	3,0
p Вишня	0	42,0	5,0	16,0	0	1	0	0,3	0,0
q Клен остролистный	0	11,5	26,0	12,5	2	1	1	1,3	1,0
r Береза пушистая	5	22,2	5,0	11,0	2	1	2	1,7	1,0
s Дуб черешчатый	0	5,0	6,3	4,0	0	0	2	0,6	0,0
t Средние...	0,5	23,5	11,2	11,1	1,0	0,7	1,0	0,9	0,6
u Ясень пенсильванский	55,0	0	45	33,3	0	2	2	1,3	3,0
v Снежноягодник	—	85	—	—	1	2	2	1,6	0,0
w Тополь черный	0	63,5	0	21,2	3	2	1	2,0	2,0
x Тополь бальзамический	62,0	21,0	0	27,6	3	3	2	2,6	3,0
y Чубушник венечный	36,0	45,0	0	27,0	3	2	1	2,0	2,0
z Сирень мохнатая	24,0	47,5	11,5	31,0	2	3	3	2,6	2,0
aa Арония черноплодная	5,0	15,4	46,5	22,3	3	2	1	2,0	1,0

*Key on separate page

[Translator's Note: Commas in tabulated numerals are equivalent to decimal points.]

TABLE 1 (cont'd)

a Виды и группы растений	b Повреждаемость в % листовой поверхности				c Степень открытия устьиц в баллах				
	d в 8 час.	e в 13 час.	f в 18 час.	g Средняя за день	d 8 час.	e 13 час.	f 18 час.	g Средняя за день	h После действия SO_2 в 8 час.
b Кизильник блестящий	31,0	66,0	5,0	34,0	3	3	2	2,6	—
c Клен татарский	12,0	53,5	69,0	44,8	2	2	2	2,0	2,0
d Калина обыкновенная	—	72,0	0	36,0	2	3	1	2,0	2,0
e Яблоня сибирская	5,0	76,0	43,0	41,3	3	3	2	2,6	3,0
f Липа мелколистная	5,0	57,3		31,1	0	2	2	1,3	0,0
g Береза бородавчатая	0,0	46,0	15,0	20,3	1	1	1	1,0	0,0
h Ирга колосоцветная	56,0	45,0	5,0	35,5	3	2	3	2,6	3,0
i Осина	47,0	31,5	47,0	43,0	3	1	2	2,0	3,0
	26,0	48,5	22,0	32,0	2,1	2,2	1,8	2,0	1,8
j Неустойчивые виды									
k Бузина красная	22,5	100	73,0	65,0	3	2	2	2,6	2,0
l Кизильник черный	8,3	100	74,0	60,6	3	3	3	3,0	3,0
m Дерен белый	16,0	95,0	80,0	63,6	0	2	2	1,3	2,0
n Ива козья	85,0	100	81,0	88,6	3	3	2	2,6	3,0
o Смородина золотистая	66,0	100	57,0	74,3	3	2	2	2,3	2,0
p Тополь серебристый	12,5	87,0	63,0	54,1	3	3	3	3,0	3,0
q Боярышник кроваво-красный	—	71,0	47,0	59,0	0	1	2	1,0	2,0
r Груша лесная	58,5	100	62,5	73,6	3	3	3	3,0	3,0
s Спирея калинолистная	14,0	92,0	93,0	66,3	1	1	2	1,3	0,0
t Рябина обыкновенная	53,0	62,5	60,0	58,0	3	2	2	2,3	3,0

TABLE 1 (concluded)

a Виды и группы растений	b Повреждаемость в % листовой поверхности				c Степень открытия устьиц в баллах				
	d в 8 час.	e в 13 час.	f в 18 час.	g Средняя за день	d 8 час.	e 13 час.	f 18 час.	g Средняя за день	h После действия SO_2 в 8 час.
u Спирея рябинолистная	45,0	83,9	57,0	61,6	2	2	2	2,0	2,0
v Барбарис обыкновенный	51,0	72,5	28,3	50,6	3	2	1	2,0	0,0
w Роза морщинистая	58,0	50,0	52,5	53,5	3	3	3	3,0	3,0
x Ива белая	87,0	21,0	80,0	60,0	3	3	3	3,0	3,0
y Лещина	87,0	95,0	95,0	92,3	2	1	3	2,0	0,0
z Спирея средняя	62,5	100	100	87,5	2	2	2	2,0	2,0
aa Айва японская	37,5	100	80,0	72,3	3	3	3	3,0	3,0
	47,7	81,0	70,0	73,0	2,35	2,23	2,35	2,33	2,1

TABLE 1

KEY:
a plant species and groups
b susceptibility to damage in % of leaf surface
c degree of opening of stoma in points
d at 8:00 a.m.
e " 1:00 p.m.
f " 6:00 p.m.
g daily average
h after action of SO_2 at 8:00 a.m.

i Resistant Species
j common elm
k Tartar honeysuckle
l spindle tree
m box elder
n bird cherry
o common lilac
p cherry
q Norway maple
r white birch
s pedunculate oak
t Average
u red ash
v snowberry
w black poplar
x balsam poplar
y coronate mock orange
z late lilac
a' black chokeberry
b' hedge cotoneaster
c' Tartar maple
d' guelder rose
e' Siberian crabapple
f' small-leaved lime
g' common birch
h' spike-flowered shadbush
i' aspen

j' Nonresistant Species
k' red-berried elder
l' black cotoneaster
m' Tartar dogwood
n' great sallow willow
o' golden currant
p' white poplar
q' red haw
r' forest pear
s' common ninebark
t' mountain ash
u' spotted-leaf spirea
v' common barberry
w' Japanese rose
x' white willow
y' filbert
z' oriental spirea
aa Japanese quince

The plant groups by resistance are very distinctly distinguished by the average indices of the degree of opening of the stoma. While it is 1.8-2.35 for the moderately resistant and nonresistant species, it is 0.7-1.0 for the resistant ones, and the daily averages: resistant 0.9, moderately resistant 2.0, nonresistant 2.33.

Thus, the slight susceptibility to damage of the first group of plants undoubtedly is connected with the slower rate of gas absorption, since the stoma are almost completely closed. On the other hand, the high susceptibility to damage of the third group of plants is connected with intensive absorption of the gas through the almost completely open stoma.

A decrease in diameter of the stomatal slit is observed in almost all species under the influence of the gas. Moreover, the reactions of the stoma to the gas was displayed better in the first group (resistant). A 40% decrease in the stomatal slit took place in them, 18% in the moderately resistant and 11% in the nonresistant ones. While the change in diameter of the stomatal slit was insignificant for gas exchange, in accordance with the rule of Stefan, in the last two groups of plants, a still greater decrease in gas exchange takes place in the resistant species under the influence of the gas. This is evidence of greater ecological plasticity of the resistant species than of the nonresistant ones.

Conclusions

1. A relation of susceptibility to damage of woody plants by sulfur dioxide on time of day and, consequently, illumination have been established. In addition, the location of species in a list by susceptibility to damage is almost unchanged with time of day.

2. Our previous conclusions on the role of number of stoma per mm^2 and their extent of opening in gas exchange rate and gas resistance have been confirmed.

3. The reactions of the stoma to the action of gas showed that the resistant species have greater ecological plasticity, which allows them to decrease the rate of gas absorption.

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